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ORIGINAL PAPER

Consistent limitation of growth by high temperature and low precipitation from range core to southern edge of European beech indicates widespread vulnerability to changing climate

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Abstract The aim of our study was to determine variation in the response of radial growth in *Fagus sylvatica* L (European Beech) to climate across the species full geographical distribution and climatic tolerance. We combined new and existing data to build a database of 140 tree-ring chronologies to investigate patterns in growth–climate relationships. Our novel meta-analysis approach has allowed the first investigation of the effect of climate on tree growth across the entire geographical distribution of the species. We identified key climate signals in tree-ring chronologies and then investigated how these varied geographically and according to mean local climate, and by tree age and size. We found that the most important climate variables significantly correlated with growth did not show strong geographical patterns. Growth of trees in the core and at the southern edge of the distribution was reduced by high temperature and low precipitation during the growing season, and by high temperatures in the previous summer. However, growth of trees growing in warmer and drier locations was more frequently significantly correlated with summer precipitation than other populations. Additionally, the growth of older and larger trees was more frequently significantly correlated with previous summer temperature than younger and smaller trees. Trees growing at the south of the species geographical distributions are often considered most at risk from climate change, but our results indicate that radial growth of populations in other areas of the distribution is equally likely to be significantly correlated with summer climate and may also be vulnerable. Additionally, tree-rings from older trees contain particular growth–climate relationships that are rarely found in younger trees. These results have important implications for predicting forest carbon balance, resource use and likely future changes to forest composition across the continent.

Keywords Fagus sylvatica · Tree-rings · Marginal populations · Growth–climate relationship · Species distribution · Climate gradient

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Introduction

Recent changes in climate are having widespread impacts on forest ecosystems, including changes in productivity, phenology, regeneration and mortality. Additionally tree populations are potentially vulnerable to changes in climate as they are stationary, usually take many decades to reach reproductive age, and because many species have relatively

poor dispersal capacity, especially in a fragmented landscape (Lazarus and McGill 2014). There is consequently a pressing need to assess the sensitivity of forests to variation in climate (Zang et al. 2014).

Dendrochronology provides a useful method for investigating the response of forests to climate variations. Radial growth has been demonstrated to be a reliable record of tree- and forest-level net primary productivity (NPP) (Latte et al. 2016), and the annual resolution and ability for retrospective sampling allow multi-decadal or multi-centennial reconstruction of annual variations in growth. Tree growth is also considered a good indicator of wider forest vitality and the sensitivity of trees to changes in climate (Dobbertin 2005). For example, tree-rings can be used to quantify the sensitivity of forest growth to climate and monitor the response of forests to environmental changes over recent decades (Dobbertin 2005; Fritts 1966; Jump et al. 2006). Furthermore, networks of tree-ring chronologies from across species' distributions can be used to identify populations that have higher or lower sensitivity to predict future climate changes, either using measurement of growth trends (Cavin and Jump 2016; Galvan et al. 2014) or by comparing the strength of growth–climate relationships (Carrer et al. 2010). Analysis of tree-ring chronologies may therefore be utilised to identify potential sources of provenances that are preadapted to climatic conditions predicted for the future, improve predictions of the impact of climate change on forest ecosystem services that are dependent on forest growth or inform efforts to conserve forest-based biodiversity (Dobbertin 2005; Gessler et al. 2007; Zimmermann et al. 2015).

In an attempt to understand variation in the sensitivity of tree and forest growth to key climate limitations such as summer drought, numerous studies have sampled along elevation gradients or within regional tree-ring networks, demonstrating spatial and elevational differences in growth response to climate (Hartl-Meier et al. 2014; Piovesan et al. 2005). However, there are important differences between elevation and latitudinal gradients which are relevant when investigating the response of a species across its distribution, including photoperiod, precipitation and genetic variation and divergence (Jump et al. 2009; King et al. 2013). There is, therefore, a need to quantify variation in the response of trees to climate across their distribution, including the core and marginal areas of the distribution and the full altitudinal range of the species. Some studies have used mixed-species networks of tree-ring chronologies to investigate continental- and hemispheric-scale patterns in the relationship between tree growth and climate. However, these have either had a dendroclimatological focus (i.e. investigating the consistency of growth–climate relationships used for climate reconstruction) (Briffa et al. 2002; Wettstein et al. 2011) or have investigated the response of forests generally to climate, rather than explicitly investigating spatial patterns in climate sensitivity across species' geographical distribution (Babst et al. 2013; Martin-Benito and Pederson 2015). These studies are, therefore, difficult to use to predict species' responses to future climate change. However, a small number of studies have explicitly investigated spatial patterns in the relationship between growth and climate across a species distribution, demonstrating the potential of this approach. For example, Chen et al. (2010) investigated growth–climate relationships in *Pseudotsuga menziesii* (Mirb.) Franco. across its distribution in western North America, showing that southern populations were better adapted to drought than their northern counterparts. de Luis et al. (2013) showed that populations at the southern distribution edge of *Pinus halepensis* Miller were more strongly limited by drought than populations from north of the Mediterranean, although they showed that southern subpopulations varied in their drought limitation of growth. The results of these studies, which indicate complex and species-specific geographical variations in the response of growth to climate, support the results of provenance trials, which have consistently reported that different subpopulations have different genetic adaptations to climate (e.g. Eilmann et al. 2014; Thiel et al. 2014). Combining analysis of distribution-wide tree-ring networks with the results from ecophysiological and other studies will improve predictions of the response of forest ecosystems to future climate change, allowing identification of populations at higher and low risk of extirpation and providing information of sources of less climatically sensitive provenances.

Here, we investigate variation in growth–climate relationships in *Fagus sylvatica* L. with: i) geographical location, ii) local climate and iii) tree characteristics such as tree age and size. *F. sylvatica* has been extensively studied due to its economic and ecological importance (Gessler et al. 2007), and various recent studies have indicated a widespread response to climate (Latte et al. 2015; Zimmermann et al. 2015). We test the potential of a novel meta-analysis approach, supplementing our own data with growth–climate relationships reported in the literature. This approach is designed to allow analysis of both raw tree-ring data, but also the inclusion of the results of previously published tree-ring studies where raw data are not available. The aim of our study is to assess the response of radial growth, a surrogate for forest productivity, to climate across the species distribution, including in regions that can be considered in the climatic and geographical core of the distribution, and marginal areas of the distribution. In particular, we focus on detecting variation in the sensitivity of growth to climate between populations, for example examining where trees are most sensitive to climate. This assessment can improve our understanding of the response

of forest growth to future climate change. Additionally, it can act as validation for models of forest growth which are used to predict the response of forests to climate change over wide geographical areas. Specifically, this study aims to investigate variation in growth–climate relationships, addressing the following key questions:

(1) Are there differences in the response of range-core and range-edge populations to key climate signals including summer drought stress?
(2) Do trees growing in marginal climates respond more sensitively to climate than trees growing close to the centre of the species climatic tolerance?
(3) Do growth–climate relationships depend on the age or size of trees?

Data and methods

Study Species

F. sylvatica is one of the most widespread broadleaved species in Europe, with a distribution stretching from southern Sweden to the mountains of southern Europe, and occurs across a wide range of environmental conditions. However, despite this wide ecological tolerance, *F. sylvatica* is considered to be a drought-sensitive species (Charra-Vaskou et al. 2012), and this may be particularly important towards its southern distribution edge where drought is more frequent (Czucz et al. 2011; Penuelas et al. 2007). Limitation of growth, regeneration, mortality and competitiveness in *F. sylvatica* have all been linked to climate and extreme events (Cavin et al. 2013; Jump et al. 2007). The sensitivity to summer drought in particular appears to be largely a result of its shallow rooting system, which is concentrated in the upper layers of the soil (Packham et al. 2012). The relationship between *F. sylvatica* radial growth and climate has been extensively investigated in Europe, but studies have either been at local scales (Friedrichs et al. 2009; Tegel et al. 2014) or for regional networks of chronologies (e.g. Di Filippo et al. 2007; Merian and Lebourgeois 2011).

Growth–climate relationships

We assembled data on growth–climate relationships in *F. sylvatica* from the published literature (Appendix S1, incorporating the published literature up to March 2014), together with 76 new sites (Cavin 2013; Hacket-Pain 2013). In dendrochronological studies, growth–climate relationships are typically quantified using the relationships between detrended tree-ring indices (RWI) and monthly climate data. The detrending process is designed to remove low-frequency variation in radial growth that is caused by changes in tree size or age and disturbance, or other changes in the biotic or abiotic environment such as stand development dynamics, while retaining high-frequency variation related to influences of annual climate conditions. The relationships between RWI and climate are usually quantified either with Pearson correlation coefficients or with response functions (a multiple regression technique that uses the principle components of the climate data to estimate RWI). While we note that response function analysis has the advantage of accounting for correlation between climate variables, we chose to focus on correlation coefficients as these were reported much more frequently in the literature. We collected information on correlations between RWI and temperature (mean monthly, mean monthly maximum and mean monthly minimum) and monthly precipitation. We could not incorporate a direct analysis of the relationship between RWI and drought as few studies report correlations with drought indices, and different studies utilise a range of drought. However, numerous previous studies have shown that correlations between RWI and precipitation and temperature record large amounts of information on the response of RWI to drought (Martin-Benito and Pederson 2015).

The significance of the correlation between RWI and climate is usually estimated using a bootstrapped resampling procedure with a confidence level of $p = 0.05$. Where significance was reported at other confidence levels, or a different method of estimating confidence was used, the results were excluded from the full dataset used for all analyses. For the majority of chronologies, correlations were reported for individual months during the year of growth up to the end of the growing season (September) and also for the previous growing season. Although correlation coefficients only represent the strength of the correlation between growth and climate, and not the slope of the relationship, Babst et al. (2013) demonstrated a strong relationship between correlation and slope. We found similar results for our dataset (Appendix S2); consequently, we consider that the correlation coefficients are a good measure of the climate sensitivity of growth. The numerical value of the correlation coefficient is often not reported in the literature, with the coefficients for each month only reported graphically. Consequently, the relationship between growth and climate at each site and for each month was recorded using three categories: significant positive correlations (coded as +1), non-significant correlations (0) and significant negative correlations (−1). While we note that this approach leads to an inevitable reduction in information about the strength of the correlations, we consider that this is compensated by the ability to include information on locations where raw tree-ring data were not available for analysis.

For each chronology, we collated additional reported data concerning the sampled forest stand. This included the location (latitude and longitude), elevation, age and mean sampled tree diameter, and information on aspect, slope and co-occurring species where this was provided. As elevation and latitude were very strongly correlated ($r = -0.836$), we calculated the elevation residual of a latitude–elevation regression and used this as a measure of relative elevation. Where mean sampled tree age was not given, we estimated the age based on the length of the RWI chronology. Additionally, we recorded details of the methodology employed in the collection, processing and analysis of the tree-ring chronologies. For full details, see Supp. Table 1.

We used the location of the chronologies to extract climate data for each site from the E-OBS database (Haylock et al. 2008). This is a publicly available gridded climate dataset with daily values at 0.25° × 0.25° resolution across Europe. We adjusted temperature for differences between the mean grid cell elevation and the elevation of the sampled stand using a temperature lapse rate of 6 °C·km-$^{-1}$, a method which has been shown to be accurate when compared to a neutral stability algorithm (Dodson and Marks 1997). Precipitation was not adjusted. In order to calculate a series of indices to characterise the mean climate at each site, we used the daily temperature and precipitation to calculate commonly used seasonal and annual climate variables, which were then used to calculate climate parameters for the period 1950–2010 (Table 1).

Description of the dataset

Our dataset includes results from 140 chronologies sampled across the distribution of *F. sylvatica* including at its northern and southern distribution limits (>57°N and <42°N, respectively) (Fig. 1a). A total of 133 chronologies reported correlations for mean monthly temperature, 84 for mean maximum temperature, 77 for mean minimum temperature and 123 for monthly sum precipitation (Appendix S1). We focused on mean monthly temperature and monthly sum precipitation in the analysis.

Three regions are poorly represented in our dataset: Scandinavia, Eastern Europe and the Italian peninsula. While we do not have data for Scandinavia, we do have an extensive dataset from the northern UK, which represents the northern region of the distribution of this species (Packham et al. 2012). An extensive network of chronologies exists for Italy (e.g. Di Filippo et al. 2007; Piovesan et al. 2005), but correlation coefficients for these individual sites have not been published. However, the southern distribution limits in the Iberian and Balkan peninsulas are well represented in our dataset, including samples from the southernmost *F. sylvatica* populations in both the Iberian and Balkan peninsulas. Our dataset contains sites from the high-elevation and low-elevation treeline in southern, central Europe, although the high-elevation treeline may be under-represented in the lowlands of northern Europe (Fig. 1b). A comparison of the mean climate values for the sampled sites with various reported climatic limits for *F. sylvatica* suggests that our dataset represents the full range of climatic conditions under which *F. sylvatica* is found (Fig. 1c). The mean chronology length of the sampled sites was 105 years (range 40–379 years). In the majority of studies in our dataset, sampling has focused on dominant and co-dominant trees. The mean sampled mean DBH was 0.49 m (range 0.15–0.94 m).

Preliminary analysis of the dataset

A preliminary analysis of the dataset was used to reveal common climate signals in the *F. sylvatica* tree-ring chronologies included in our dataset, enabling us to focus the study of the key climate signals in this species. For most months, correlations between monthly temperature and RWI were negative, and for two periods significant

Table 1 Climate parameters calculated for each site included in the database

Climate parameter	Description (units)
T	Mean annual temperature (°C)
T_{max}	Mean temperature of the warmest month (°C)
T_{min}	Mean temperature of the coldest month (°C)
P	Sum of annual precipitation (mm a^{-1})
P_s	Sum of summer precipitation (May–August inclusive) (mm a^{-1})
P_w	Sum of winter precipitation (Dec–Feb inclusive) (mm a^{-1})
I_c	Continentality index, T_{max}–T_{min} (°C)
PET	Sum of annual potential evapotranspiration (Thornthwaite method) (mm a^{-1})
SPET	Sum of summer potential evapotranspiration (May–August inclusive) (mm a^{-1})
Aridity index	P/PET (unitless index)
Summer aridity index	P_s/SPET (unitless index)

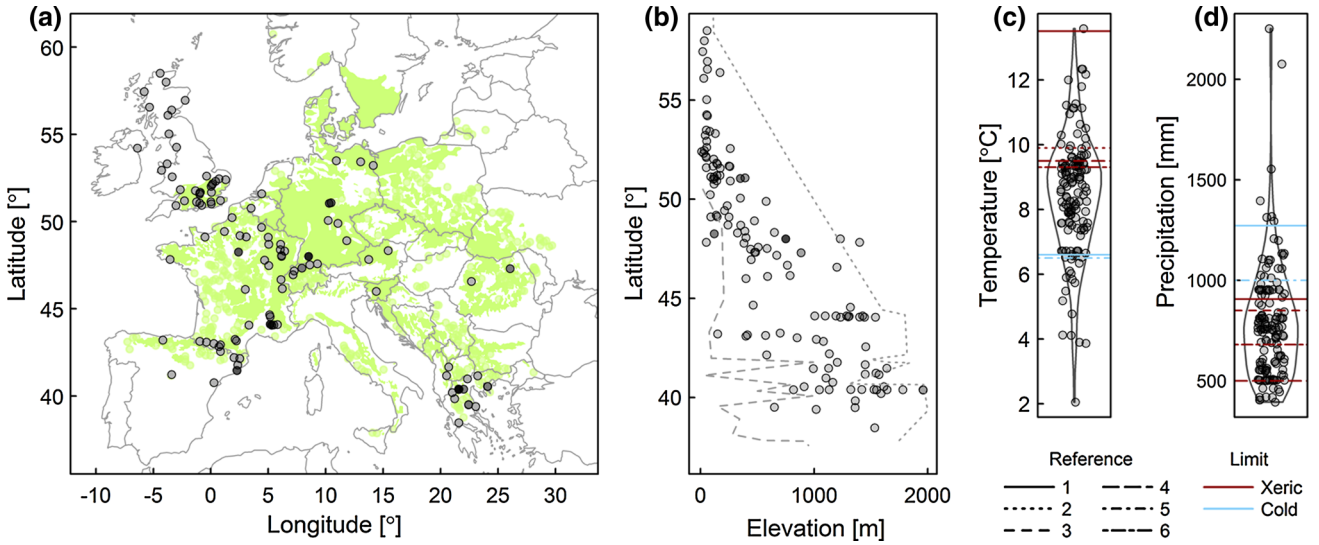

Fig. 1 Location and mean annual climate of the sites included in the dataset. **a** The distribution of sampled sites and the geographical distribution of *F. sylvatica* (EURFORGEN 2009). We note that this distribution map does not include the extensive naturalised *F. sylvatica* populations in the UK, and we follow the recommendation of Packham et al. (2012) in considering this region climatically suitable for *F. sylvatica*. *Darker points* indicate locations with multiple chronologies included in the dataset (i.e. sites sampled at different elevations). The map is unprojected. **b** The same data as **a**, but with the sampled sites plotted according to latitude and elevation. The *dotted* and *dashed* lines show variation in the upper and lower treeline elevation for F. sylvatica with latitude. Treeline elevations were taken from Fang and Lechowicz (2006), Zianis and Mencuccini (2005), Pezzi et al. (2008) and Penuelas and Boada (2003). **c** The mean annual temperature of the sampled sites (data taken from E-OBS gridded dataset, adjusted for elevation). The *horizontal lines* refer to various published climatic limits for beech. *1* Fang and Lechowicz (2006), *2* Lakatos and Molnár (2009), *3* Kölling (2007, cited Matyas et al. 2009) (warm–humid limit), *4* Kölling (2007, cited Matyas et al. 2009) (cool-dry limit), *5* Penuelas and Boada (2003), *6* Czucz et al. (2011). **d** as for **c** but for annual sum precipitation (not adjusted for elevation)

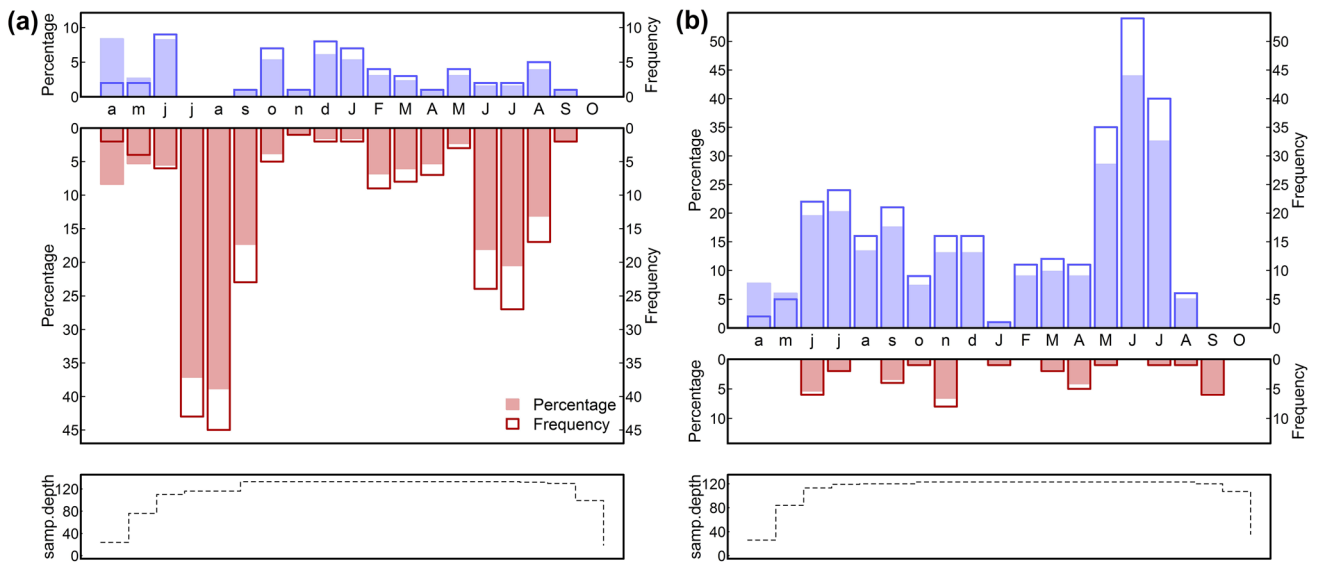

Fig. 2 Frequency of reported significant correlations between RWI and monthly climate. The *top* panels show the frequency of significant positive correlations, the *middle* panel the frequency of significant negative correlations and the *bottom* panel the number of sites reporting correlations for each month. **a** Mean monthly temperature. **b** Monthly precipitation sum

negative correlations were particularly frequently reported (Fig. 2). Correlations with mean temperatures in the summer months during the year of growth were frequently significantly negative: June (18.8 % of chronologies), July (19.7 %) and August (12.1 %). However, significant correlations were more frequently reported for late summer months of the year prior to growth: July (37.1 %), August (38.8 %) and September (17.3 %). For precipitation, significant correlations were usually positive, particularly during the early and mid-summer months: May (28.7 %),

June (44.7 %) and July (32.8 %) (Fig. 2). Significant correlations between monthly precipitation of the previous year and RWI were consistently negative, but we found no peak in significant correlations for the months of July–September equivalent to that for mean temperature. The overall pattern of significant correlations for mean maximum temperature was broadly similar to that for mean temperature, although correlations with current and previous summer temperature were more common as a percentage of all chronologies (Appendix S3). Significant correlations with mean minimum temperature were much less common, but significant correlations with previous summer temperature were still the main signal.

For the analysis of growth–climate relationships in the rest of this study, we focused on the three main climate signals: previous summer temperature (July–September, $T_{\mathrm{SUM}\ -1}$), current summer temperature (June–August, T_{SUM}) and current summer precipitation (May–July, P_{SUM}). For each chronology, significant correlations were pooled so that chronologies with at least one positive (or negative) significant correlation during each period were classed as having a positive (or negative) significant correlation for the period. We pooled the correlations into these three periods to reflect the dominant climate signals in Fig. 2 and to simplify the presentation of the results. However, all analyses were repeated with the individual months to confirm that this pooling did not create spurious results. While this approach will reduce our ability to investigate variations in seasonal signals (Piovesan et al. 2005), it allows us to focus on the most prevalent climate signals for this species (summer temperature and precipitation). Additionally, pooling correlations for these months counteracts the influence of covariation in the climate data for different months.

Analysis of growth–climate relationships

To test whether sampled populations close to the distribution limit have different responses to climate compared to those within the core of the range, and to see whether different marginal areas responded differently to climate, we mapped the correlation classes according the location of the sampled sites. As our data do not allow a comparison of the magnitude of correlation coefficients for different regions, we instead used the relative frequency of significant correlations to investigate differences between regions. We also tested for differences in the latitude and elevation of the three correlation classes (significant positive, non-significant and significant negative). To investigate whether growth–climate relationships changed according to mean climate at the site, we also tested for relationships between the eleven mean climate variables calculated for each site (Table 1) and the three correlation classes. Finally, we investigated any effect of tree characteristics by testing whether growth–climate relationships were related to the age and size of the sampled trees.

As with all meta-analyses, there are some differences in methodology between the studies that we compiled for our analysis. To ensure that these differences did not influence the results of our analysis, we repeated all analyses for a subsample of the full dataset that included only our own chronologies, sampled and analysed with a consistent methodology (referred to as the "subset dataset", for details, see Supp. Table 1). Additionally, the full dataset was split into a series of subsamples and the consistency of our results was tested across these subgroups. We split the full dataset into four nominal regions with approximately equal numbers of sites (UK, central and northern Europe, southwest Europe, southeast and east Europe), low and high relative elevation classes, younger and older chronology ages, and larger and lower mean sampled DBH classes.

Results

Geographical patterns in growth–climate relationships

In contrast to expectations, we did not find a clear spatial pattern in the distribution of significant correlations between RWI and T_{SUM}, such as a clustering of negative correlations at southern latitudes (Fig. 3). In the two well-sampled regions at the southern distribution limit of this species, tree growth was no more frequently significantly negatively correlated with high summer temperatures than in the core or northern parts of the distribution, despite higher temperatures and lower precipitation in these regions. Additionally, we expected that the most northerly sites would represent a cluster of positive correlations (indicating that growth is favoured by warm summer temperatures). Three of the seven significant positive correlations were located in northern Scotland, supporting this hypothesis, but overall we found no statistically significant difference in the median latitude of the three correlation classes (Kruskal–Wallis test, $\chi^2 = 2.304$, $\mathrm{df} = 2$, $p = 0.316$). Additionally, we did not find a significant difference in the median relative elevation of the three correlation classes (Kruskal–Wallis test, $\chi^2 = 1.087$, $\mathrm{df} = 2$, $p = 0.581$), implying that tree growth at both high and low elevations is sensitive to limitation by high summer temperatures. We found similar results for $T_{\mathrm{SUM}-1}$, with no significant variation in the frequency of significant correlations with either latitude or residual elevation (Appendix S4).

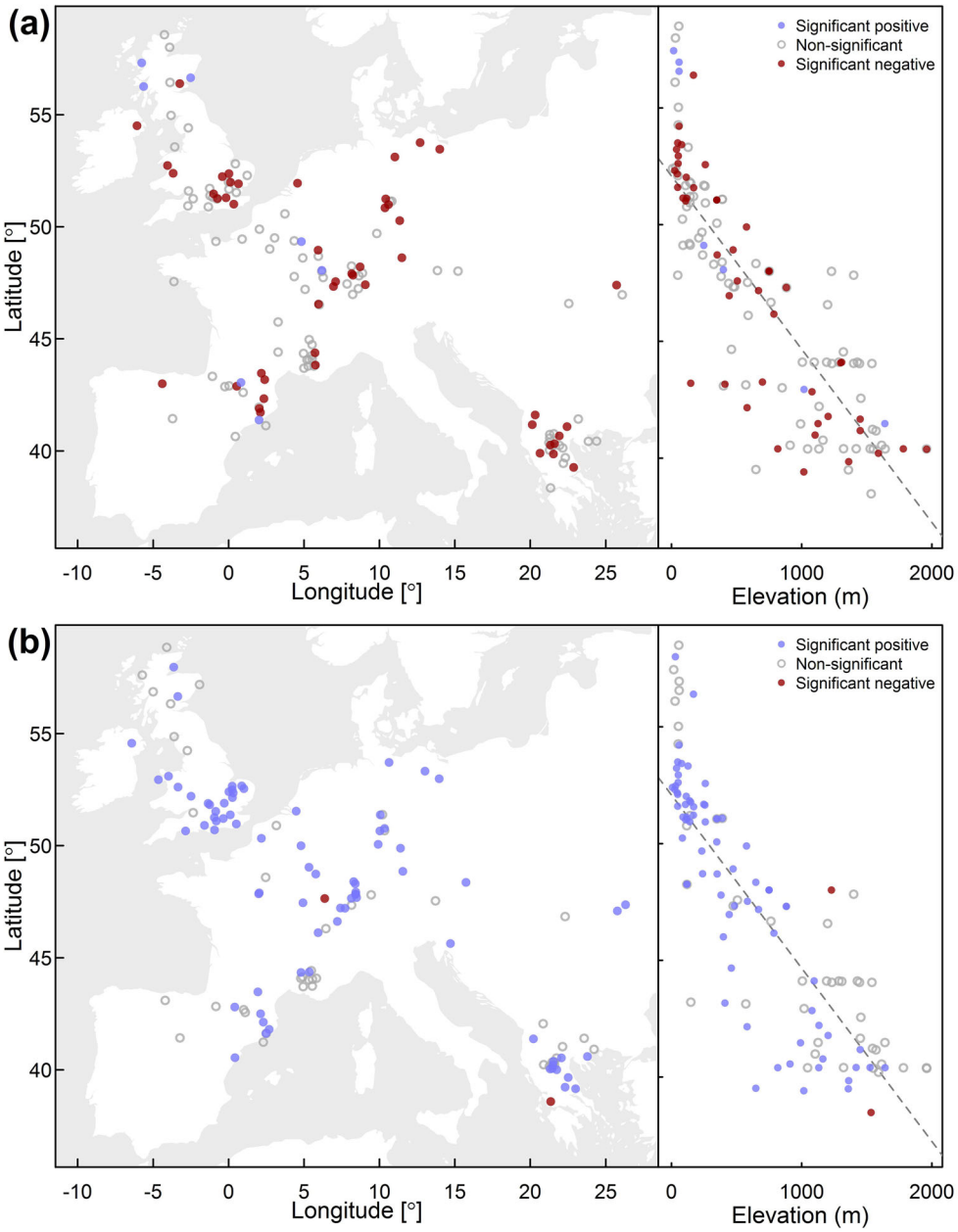

Fig. 3 Maps showing the spatial distribution of significant and non-significant growth–climate relationships for *Fagus sylvatica*. The *right-hand* panel shows the same data, but with the sampled sites plotted according to latitude and elevation. **a** T_{SUM} (current summer temperature). **b** P_{SUM} (current summer precipitation). The *dashed line* shows the linear relationship between the latitude and elevation of sites. Sites have been plotted with a small amount of jitter in the *left-hand* panel, but not in the *right-hand* panel. This jitter was added in order to reduce the over plotting in cases where individual sites have the same, or very similar, locations. The maps are unprojected

For P_{SUM}, geographical patterns did exist, but were quite weak (Fig. 3). There was a significant difference in the median latitude of the three classes, with the highest median latitude for significant positive correlations ($-1 = 43.2°$, $0 = 44.1°$, $1 = 48.7°$, Kruskal–Wallis test, $\chi^2 = 7.163$, df $= 2$, $p = 0.028$). Surprisingly, this would indicate that the growth of trees at higher latitudes is more likely to be strongly limited by the availability of summer precipitation than for trees growing further south. However, this trend was not consistent within the different geographical regions (Appendix S5), where the trend was in fact reversed (i.e. within the four regions, positive correlations tended to be more likely at lower latitudes). The significant relationship found in the full dataset (Fig. 3) appeared to be caused by a sample bias, with a large number of sample sites at high elevation in southern Europe with few positive correlations, and under-sampling of the equivalent high latitude sites in northern Europe where positive correlations might also be expected to be less frequent. Across Europe, significant positive correlations between RWI and summer precipitation were more frequent at lower elevations, with a significant difference in median residual elevation between the classes (Kruskal–Wallis test, $\chi^2 = 23.355$, df $= 2$, $p \leq 0.001$). This observation was consistent across the regions, but was stronger in southern Europe (Fig. 3 and Appendix S6). In summary,

significant correlations between RWI and summer temperature (negative) and summer precipitation (positive), both considered indicators of a drought limitation on growth, did not show strong geographical patterns observed in some previous studies (Chen et al. 2010; de Luis et al. 2013), particularly for summer temperature. This was despite the strong environmental gradients found across our study area (Fig. 1).

In addition to investigating variation in the relationship between growth and climate with latitude, we also compared the two well-sampled regions at the southern distribution edge of the species. Both showed approximately equal percentages of sites with significant correlations between growth and summer temperature and precipitation, indicating that tree growth in these two regions shares broadly similar sensitivity to summer weather conditions (Fig. 3).

Variation in growth–climate relationships with mean climate

In addition to testing for geographical patterns in growth–climate relationships, we also tested for the effect of local mean climate. Kruskal–Wallis tests and Wilcoxon tests were used to test for significant differences in mean climate indices between the correlation classes (Table 2). For T_{SUM} and T_{SUM-1}, no significant differences in mean climate indices were found between the correlation classes. While we found no effect of mean climate conditions on the probability of significant correlations between tree growth and summer temperature, we did find effects for correlations with summer precipitation. Significant positive correlations between growth and summer precipitation were associated with higher temperature (T, PET) and lower water availability (aridity index, SPEI) (Table 2), showing that the RWI of trees growing in warmer and more arid sites were more frequently significantly correlated with summer precipitation. For example, of the ten sites with the highest mean annual temperature, tree growth at eight was significantly positively correlated with summer precipitation, while only one of the ten coolest sites had a significant positive correlation.

Figure 4 shows the distribution of correlations of the three different classes within a temperature–aridity index space. The bagplots show the bivariate median for each class and a "bag" that incorporates 50 % of all observations, and can be considered a bivariate equivalent to the interquartile range in a boxplot. The median and bag of the significant positive correlations were shifted relative to the non-significant correlations, so that significant positive correlations between RWI and P_{SUM} were more likely at sites with higher mean annual temperatures and lower aridity index (Fig. 4). In the analysis of individual months, this difference was strongest for P_{MAY} and weakest for P_{JUL} (Appendix S7), indicating that early summer

Table 2 Results (p values) of Kruskal–Wallis and Wilcoxon tests for climate indices (see Table 1) according to the correlation significance

Climate index	T_{SUM}	P_{SUM}	T_{SUM-1}
T	0.995 (0.946)	**0.001* (<0.001*)**	0.164
T_{max}	0.495 (0.878)	0.124 (0.053)	0.789
T_{min}	0.333 (0.663)	0.086 (0.083)	0.223
P	0.072 (0.289)	0.114 (0.050)	0.884
P_s	0.128 (0.700)	0.750 (0.510)	0.901
P_w	0.019 (0.110)	0.008 (0.009)	0.657
I_c	0.068 (0.534)	0.730 (0.542)	0.104
PET	0.973 (0.886)	**<0.001* (<0.001*)**	0.048
SPET	0.226 (0.191)	**<0.001* (<0.001*)**	0.415
Aridity index	0.055 (0.268)	0.006 **(0.004*)**	0.590
Summer aridity index	0.086 (0.624)	0.536 (0.276)	0.945

Kruskal–Wallis tests were applied to T_{SUM} and P_{SUM} (three significance categories) and Wilcoxon tests to T_{SUM-1} (two categories). As some correlation classes included small numbers of observations, Wilcoxon tests were also applied to a subset of the data where the category with lowest number of observations was removed, i.e. T_{SUM} (significant positive correlations removed, $n = 7$) and P_{SUM} (significant negative correlations removed, $n = 2$). The p values for these tests are given in parentheses. Results in bold represent significant results (Bonferroni correction applied, significance at $p = 0.005$)

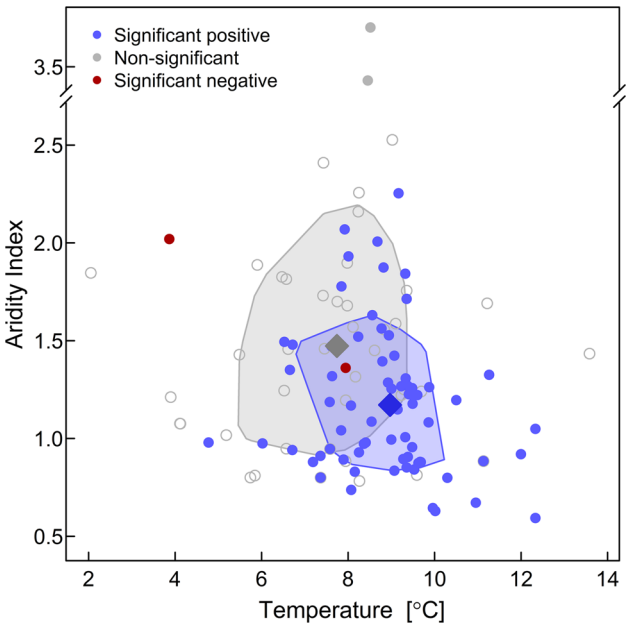

Fig. 4 Bagplots showing the significance of correlations between RWI and P_{SUM} in relation to the mean climate of the sampled site. A bagplot is bivariate generalisation of the boxplot. The *solid diamond* represents the estimated bivariate median. The *shaded* "bag" is calculated to include 50 % of individual data points (analogous to the interquartile range). All individual sites are also plotted. Note that a bagplot was not plotted for significant negative correlations as there were only two observations

precipitation is a particularly important limitation on tree growth at the warmest and driest sites.

Variation in growth–climate relationships with tree age and size

Chronology age and the mean sampled DBH of the sampled trees did not differ between the correlation classes for T_{SUM} or P_{SUM}, but sites with significant negative correlations between RWI and T_{SUM-1} had significantly older and larger sampled trees than those with non-significant correlations (Table 3 and Fig. 5). This disparity shows that the growth of stands with older and larger trees responds differently to previous summer temperature than younger and smaller trees. For example, of the 61 sites with mean chronology age <100 years, only 18 (30 %) had significant negative correlations for T_{SUM-1}, in comparison with the 55 sites with mean chronology age >100 years, where 39 (71 %) had significant negative correlations (note that although 133 sites reported correlations for mean temperature, only 116 included analysis for summer months in the year prior to growth, see Fig. 2). The effect of age and size was consistent across the four geographical regions, and across the other subgroups and the subset dataset (Appendix S8 and S9). The relationship between chronology age, mean sampled DBH and correlation classes was strongest for the individual month of T_{JUL-1} and weakest for T_{SEP-1} (Appendix S10).

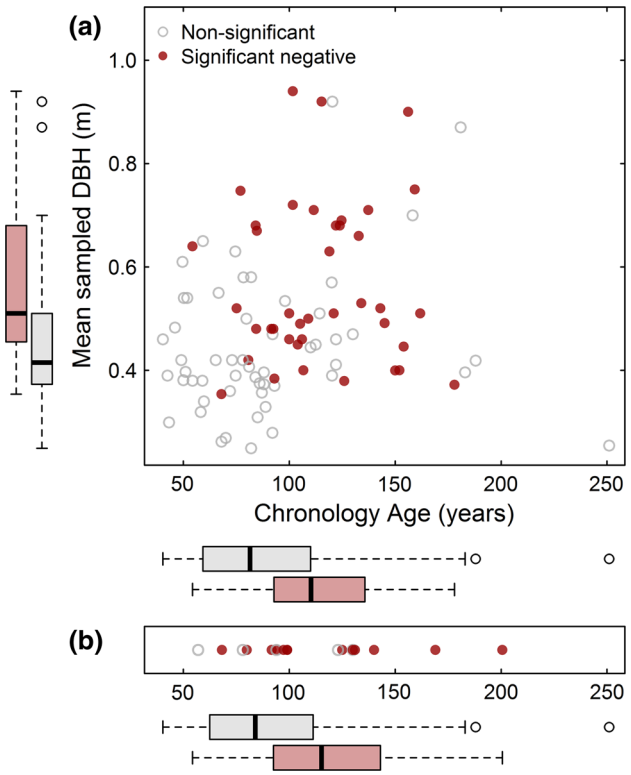

Fig. 5 Plot showing the significance of correlations between RWI and T_{SUM-1} in relation to the chronology length and mean sampled DBH of the site. **a** Sites where age and DBH reported. **b** Additional sites where DBH was not reported. Note that the boxplot includes all sites plotted in **a** plus the additional sites. Differences in median chronology age and mean sampled DBH are all significant (Mann–Whitney U test, $p < 0.001$)

Discussion

Using published and new unpublished growth–climate relationships from a distribution-wide network of tree-ring chronologies, we investigated growth–climate relationships in *F. sylvatica* and how the growth response of this species to climate varied between populations. For the first time, we specifically tested for variation in growth–climate relationships across the geographical and climate space occupied by the distribution of a species and according to the age and size of the sampled trees. Previous work has shown that *F. sylvatica* is a highly drought-sensitive species, with growth particularly strongly limited by summer drought at low elevations in southern Europe (Di Filippo et al. 2007). We wanted to investigate whether a distribution-wide network of tree-ring chronologies could be used to detect an equivalent pattern with latitude (i.e. increased sensitivity to drought towards the southern distribution edge). Furthermore, we were interested to see whether such a large dataset could be used to identify characteristics that might make populations more or less sensitive to climate (and by extension, changes in climate), such as mean local climate conditions or tree size and age. The key features we identified for the distribution-wide climate–growth relationships for *F. sylvatica* were: (1) The three most important climate signals are previous summer temperature (the most common signal), current summer temperature and current summer precipitation; (2) no strong latitudinal

Table 3 Results (p values) of Kruskal–Wallis and Wilcoxon tests for stand characteristics according to the correlation significance

Stand characteristic	T_{SUM}	P_{SUM}	T_{SUM-1}
Chronology age (years)	0.566 (0.851)	0.070 (0.457)	**<0.001***
Mean sampled DBH (cm)	0.354 (0.843)	0.713 (0.667)	**<0.001***

Kruskal–Wallis tests were applied to T_{SUM} and P_{SUM} (three significance categories) and Wilcoxon tests to T_{SUM-1} (two categories). Also note that Age and DBH are weakly correlated ($r = 0.178$). As some correlation classes included small numbers of observations, Wilcoxon tests were also applied to a subset of the data where the category with lowest number of observations was removed, i.e. significant positive correlations removed for T_{SUM} ($n = 7$) and significant negative correlations removed for P_{SUM} ($n = 2$ for Age, $n = 1$ for DBH). The p values for these tests are given in parentheses. Results in bold represent significant results (Bonferroni correction applied, significance at $p = 0.025$)

gradient of significant correlations between tree growth and climate exists, with no clustering of significant correlations between growth and summer temperature or precipitation at southern sites, but some evidence of positive responses to summer temperature at the highest latitude sites; (3) the positive effect of summer precipitation on tree growth was strongest at the most xeric sites, but the negative effect of higher summer temperatures did not vary according to mean climate; (4) the negative effect of previous summer temperature on growth was significantly positively associated with tree age and tree size.

One of the fundamental principles of dendroecology and dendroclimatology is that tree populations in marginal regions are more sensitive to climate than those in core regions, with more interannual variability in growth and stronger relationships between growth and limiting climate factors, particularly summer drought (Fritts 1966). This principle has been demonstrated for conifers (Carrer et al. 2010; de Luis et al. 2013; Linares et al. 2009) and also to a more limited extent in broadleaved species such as *F. sylvatica*, although research has focused on elevation transects or regional networks of sites. For example, studies have shown that *F. sylvatica* at low elevations is more sensitive to summer drought than at high elevations (Di Filippo et al. 2007; Hartl-Meier et al. 2014). In our analysis, we reported similar findings in southern and central Europe, with significant positive correlations between growth and summer precipitation in low-elevation sites, although we did not find any patterns for temperature. Importantly, however, we did not find an equivalent pattern with latitude, such as a higher frequency of significant correlations at low latitude, low-elevation sites, close to the species distribution limit (Fig. 3). In fact, we found that sites towards the northern limits of the range and particularly within the core of the range were as equally likely to show significant correlations indicative of summer drought limitation on radial growth as at the southern margin of the distribution. This has important implications for the future response of this species to climate change, as it indicates that the strongest effects of drought are not necessarily restricted to trees at the equatorial margins of species distributions. Indeed, even trees in the more northern parts of the range may be at negatively impacted from long-term changes in climate, or more frequent extreme weather events (Latte et al. 2015). For example, the cluster of significant correlations in the southern UK (Fig. 3) indicates that *F. sylvatica* populations in this region may be particularly sensitive to future increases in summer drought stress. This was predicted by Broadmeadow et al. (2005), and similar results have been reported in *Quercus robur* L., where growing season drought is a significant climate stress across the species geographical distribution and is not restricted to marginal populations (Drobyshev et al. 2008; Rozas 2005).

While our analysis does not support the hypothesis that geographically marginal populations are more sensitive to summer temperature and precipitation (and therefore we assume summer drought stress), we do show that significant positive correlations between RWI and summer precipitation are more likely in warmer and more arid sites where summer drought stress is presumed to be greater (Fig. 4). This result is similar to those reported by de Luis et al. (2013), who showed that the growth of *Pinus halepensis* in drier and warmer regions was more sensitive to mean annual temperature. Our results for *F. sylvatica* therefore show that trees growing in *climatically marginal* regions (rather than *geographically marginal* regions) are more sensitive to climate. The lack of strong geographical patterns in significant growth–climate relationships, despite strong climate gradients across Europe, is consistent with a high degree of variation in the response of this species to climate. This is in agreement with the results of ecophysiological studies (Fotelli et al. 2009) and provenance trials (Robson et al. 2013), which have demonstrated weaker responses of southern populations to identical or comparable drought conditions. Using our data, we are not able to establish whether this plasticity in response to climate across the species range is due to local genetic adaptation (i.e. drought-adapted southern European provenances) or acclimation to local conditions. Common garden experiments of phenology (Robson et al. 2013), seedling response to drought (Thiel et al. 2014) and water-conducting anatomy (Eilmann et al. 2014) have suggested that *F. sylvatica* populations have a high degree of adaptation to local climate. *F. sylvatica* also exhibits the potential for acclimation to changes in climate over timescales up to several years (Wortemann et al. 2011).

An alternative and non-genetic explanation for our finding that geographically marginal populations do not appear to be more sensitive to climate is that habitat selection is likely to have occurred more strongly at the range edge. In these regions, populations might be expected to occupy only a restricted suite of the environment occupied by the species elsewhere in the range. Consequently, populations at the range edge do not appear to be climate-sensitive because they are already absent from climatically marginal sites. In essence, at the equatorial range edge many sampled populations are already "climate relicts, occupying locations where local features interact to ameliorate the regional climate" (Cavin and Jump 2016; Hampe and Jump 2011). In contrast, more frequently benign conditions in the distribution core allow the species to occupy (and be sampled at) a wider range of environments, and consequently, the species displays similar climate signals present at the range edge, despite a less extreme regional climate.

In addition to our analysis of growth–climate relationships for climate conditions during the year of growth, our dataset also allowed investigation of correlations between

growth and previous summer climate. Significant correlations between RWI and previous summer temperature were more common than any other correlation (Fig. 2). This finding was in agreement with the results of Babst et al. (2013) using an independent dataset of *F. sylvatica* chronologies from Germany. Significant correlations between RWI and previous summer temperature are also frequently observed for other species, including *Picea abies*, *Pinus sylvestris* and *Pinus nigra* (Babst et al. 2013; Wettstein et al. 2011). This lagged correlation between the growth of *F. sylvatica* (and potentially other species) and previous summer temperature has been explained as a carry-over effect caused by carbohydrate depletion in unfavourable (warm) years leading to a growth reduction in the following year. An alternative explanation is that the lagged correlations between growth and previous summer temperature are a result of weather-cued masting events (Drobyshev et al. 2010; Piovesan and Schirone 2000). This mechanism proposes that as mast events are cued by warm temperatures in the previous summer, and mast years are themselves associated with a strong decline in growth, narrow rings will be associated with warm previous summer temperatures. Consequently, strong statistical relationships between previous summer temperature and growth result, at least in part, from an interaction between weather conditions, seed production (mast events) and growth (Hacket-Pain et al. 2015a). The finding that negative correlations between RWI and previous summer temperature were more frequently significant in sites with older and larger trees may support this masting-related mechanism. As older trees have been shown to increase investment in reproduction relative to growth (Genet et al. 2010), the effect of masting on tree growth may increase with tree age (Hacket-Pain et al. 2015b). In contrast, older trees allocate more carbon to storage and have larger overall stores of carbon (Genet et al. 2010; Sala et al. 2012), implying that carbohydrate depletion during unfavourable conditions should have a smaller effect on growth the following year in older (and larger) trees (the carry-over mechanism).

Our observation that mean chronology age influences the frequency of significant (strong) correlations between RWI and previous summer temperature is also relevant to current research investigating climate signal age effects (CSAE) in tree-ring chronologies (Esper et al. 2008). Numerous studies have demonstrated that the strength of growth–climate relationships is dependent on tree age (Copenheaver et al. 2011). Various physiological explanations have been proposed for size and age effects, including changes in hydraulic resistances or photosynthetic rates (for a comprehensive review, see Carrer and Urbinati 2004). CSAE have significant implications for tree-ring-based reconstructions of climate, as they imply that when the mean age of the sampled trees varies through the chronology (as is usually the case due to constraints of sampling), the sensitivity of the sampled chronology to the climate signals being reconstructed may vary. Our results suggest that climate signals in tree-ring chronologies may also vary with life history—i.e. changes in reproductive effort and subsequent reproductive-related climate signals. While we note that *F. sylvatica* is not generally used for climate reconstructions, importantly, we show CSAE across a much larger number of sampled sites than previous studies. However, these results should be interpreted with caution as our data only consider the mean age of the trees sampled in a stand; analysis at the individual tree level will allow more robust conclusions to be drawn regarding the effect of tree age on growth–climate relationships.

We have presented the first study to investigate variation in the sensitivity of tree growth to climate across a broadleaved species' entire geographical distribution, using a novel meta-analysis approach incorporating data from 140 tree-ring chronologies from across Europe. For the first time, we have been able to compare the climate sensitivity of mature trees of this species growing in marginal areas at the edge of the species distribution with populations in the core of the distribution. Surprisingly, our results indicate that these *geographically marginal* forests are not significantly more sensitive to summer drought than populations in the core of the distribution, although we have shown that trees growing in *climatically marginal* areas (warmer and more arid climate) are more likely to have significant summer precipitation limitation on growth. We stress that our results do not mean that *F. sylvatica* at the distribution edge is not at risk from future climate change, but that some populations in the core regions of the distribution may be equally at risk as southern populations. We also note that we do not assess demographic changes which ultimately determine the response of species, and our growth–climate analysis is limited to dominant and codominant trees. These trees are likely to be the most stable and resilient, and seedlings and saplings mortality may ultimately lead to the loss of range-edge populations. Furthermore, the growth–climate relationships we have investigated in this study quantify how annual growth responds to interannual variations in climate, and do not necessarily contain information on how trees will response to expected changes in future climate, including the existence of tipping points (Cavin et al. 2013). Additionally, we have also shown that the sensitivity of tree growth to previous summer temperature (the most commonly reported significant growth–climate relationships in this species) is highly dependent on tree size and age, consistent with a masting-related mechanism being responsible for this climate signal in tree-ring chronologies.

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